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ENVIRONMENTAL GRADIENTS AND BENTHIC MACROINVERTEBRATE DISTRIBUTIONS IN A SHALLOW NORTH CAROLINA ESTUARY

Alexander J. Chester, Randolph L. Ferguson and Gordon W. Thayer

ABSTRACT

Multivariate statistical analyses were employed to identify environmental gradients and describe distributional patterns of benthic macroinvertebrates (numbers, biomass and species composition) in subtidal sediments of a shallow, southeastern United States estuary. Biomass and numbers of individuals increased significantly along a major estuarine gradient from fine anaerobic sediments, rich in organic matter and pheopigment (upper estuary) to coarse aerobic sediments, high in ATP and chlorophyll (lower estuary). A second environmental gradient within the lower estuary linked high numbers of invertebrates to depositional areas near salt marshes and low numbers to turbulent regions adjacent to deep, tidally-scoured channels. Invertebrate species composition was spatially associated with both environmental gradients.

Estuaries of the mid-Atlantic and southeastern United States are productive nursery grounds for a variety of commercially important fish and shellfish including menhaden (*Brevoortia tyrannus*), spot (*Leiostomus xanthurus*), flounder (*Paralichthys* spp.), blue crab (*Callinectes sapidus*), shrimp (*Penaeus* spp.) and oysters (*Crassostrea virginica*) (Wolfe et al., 1973). Because many of these estuaries are shallow, the benthic invertebrate community may represent the dominant trophic pathway leading to higher organisms (Williams et al., 1968; Hyle, 1976). Assessing the impact of benthos on fishery yield requires data on benthic production and community structure over varied substrates, the influence of bacteria and meiofauna on net energy flow, and feeding requirements of fish (Mills, 1975). This approach suggests complex relationships among biological and physico-chemical variables that have often been difficult to demonstrate statistically (Poore and Mobley, 1980).

Between 1972 and 1975, staff of the National Marine Fisheries Service Laboratory at Beaufort, North Carolina conducted a series of eight benthic surveys to describe 13 sediment, microbial and invertebrate parameters in the Newport River, a shallow, seawater-dominated, North Carolina estuary. Preliminary information on biomass and activity of microbes (Ferguson and Murdoch, 1975), and on distributions of macroinvertebrates (Thayer et al., 1975) and nekton (Kjelson and Johnson, 1978) were presented without attempting to produce an integrated view of the benthic environment. We here consider the full data set to statistically evaluate relationships among physico-chemical and biological parameters.

Recently, multivariate statistical techniques have been applied to quantify interactions between benthic organisms and environmental factors (Hughes and Thomas, 1971; Boesch, 1973; Mountford et al., 1977; Moore, 1979; Biernbaum, 1979; Ivester, 1980). These studies demonstrate shifts in species assemblage patterns related to spatial differences in sedimentary characteristics. Generally, emphasis is placed on identification of organism groupings. Complementary descriptions of the benthic environment either are qualitative or limited to consideration of sediment particle size and, occasionally, organic carbon content. We use two multivariate approaches to examine correlations among these sedimentary pa-

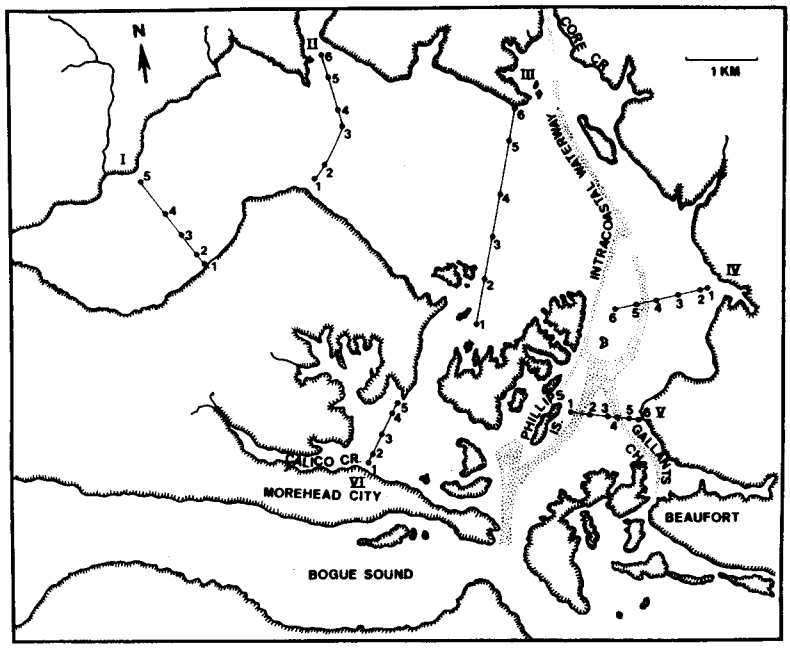


Figure 1. Map of the Newport River estuary showing the sampling locations. Transect numbers are designated by Roman numerals. Stippled areas are dredged or naturally maintained channels. Approximate position of Beaufort, N.C., is 34°43.1'N, 76°39.5'W.

rameters and add indices of autotrophic and total microorganism biomass. Ordination techniques (principal component and canonical correlation analyses) are used to define environmental gradients that are related to patterns of invertebrate biomass, numerical abundance and species number. Classification procedures (cluster analysis) are used to categorize and map estuarine areas according to invertebrate species composition. We combine results from these analyses to demonstrate spatial relationships between the environment and invertebrate assemblages.

METHODS

Habitat Description

The Newport River estuary (Fig. 1), located between Morehead City and Beaufort, North Carolina, drains a small watershed (340 km²) consisting primarily of pine-cypress pocosins, low-lying pine forests, and agricultural lands (Wolfe, 1975). It is relatively small (31 km²) and shallow (mean depth < 1 m at mean low tide). The lower estuary contains some deeper areas periodically dredged or naturally maintained. The intracoastal waterway passes on the western side of Phillips Island, across the estuary, and into Core Creek. It is intersected northeast of the island by Gallants Channel. Both channels are dredged to a depth of 4–5 m every 2 or 3 years. Natural channels and deeper basins maintained by tidal scouring (Bird, 1970) are east of, and generally parallel to, the intracoastal waterway. Water in the estuary is usually unstratified because of wind and tidal mixing. High tide salinities and temperatures ranged from 15–38‰ and 5–35°C during the study, but fluctuations as large as 20‰ and 6°C within 1 h have been measured in the freshwater dominated portion (Rice and Ferguson, 1975). Extensive salt marshes dominated by *Spartina alterniflora* occupy much of the broad intertidal and supratidal region.

Field and Laboratory Procedures

Thirty-four subtidal stations along six transects were sampled eight times between 1972 and 1975 (Fig. 1 and Table 1). Depth, temperature, and salinity were recorded. Samples for microbial analysis

and determination of sediment particle size and organic content were collected with a 2.8-cm-diameter hand coring device described by Ferguson and Murdoch (1975). Sediment was subsampled at 0, 5, and 15 cm, extracted in the field, frozen, and subsequently measured for ATP (adenosine triphosphate), chlorophyll *a*, and pheopigment concentrations (Ferguson and Murdoch, 1975). Additional samples (0–5-cm stratum) were dried to constant weight, and duplicate subsamples were analyzed for particle size (Bouyoucos, 1936). Organic content of dried sediment was taken as loss of weight upon ashing (500°C, 36 h); organic carbon was determined with the wet oxidation technique (Morgans, 1956).

Invertebrates were collected with a modified Knudsen sampler (Thayer et al., 1975). Replicate, 30.5-cm-diameter cores were obtained in the upper 30–40 cm of sediment. Samples were sieved through a 1.2-mm-mesh screen to facilitate processing, though this mesh size is larger than recommended for smaller volume samples (Birkett and McIntyre, 1971). Organisms separated from coarse debris by flotation were frozen for later analysis. All animals were identified, counted, dried to constant weight at 100°C, decalcified in 20% HCl (Thayer et al., 1973), and ashed at 500°C for 36 h to determine organic content (ash-free dry weight).

Data Reduction and Analysis

Data were averaged over the eight sampling dates to provide a set of 34 station observations. Thirteen parameters including water depth, salinity, six sediment variables, two microbial variables, and three summary invertebrate variables were analyzed. Sediment variables were sand, silt, clay, organic matter, organic carbon (all expressed as percent dry weight), and pheopigment (an index of decomposing plant material). Microbial variables were ATP (an index of total microbial biomass) and chlorophyll *a* (an index of autotrophic biomass). Invertebrate variables included total numbers and biomass of organisms and total number of species present. All samples or data were integrated over the upper 5 cm of sediment, except chlorophyll (upper few mm) and invertebrates (upper 30–40 cm). Except for salinity and depth, all variables were transformed with either a $\log(X + 1)$ or an arcsine transformation for percentage data (Sokal and Rohlf, 1969). We employed both ordination and classification procedures. Ordination is best suited for creating composites of multiple variables for further statistical analysis, while classification is more appropriate for mapping species distributions (Goodall, 1978). The combination of these two approaches is desirable, given the complexity of the data set and the attributes of each approach (Clifford and Stephenson, 1975).

Correlations between and among environmental and summary invertebrate variables were analyzed by multivariate ordination procedures. Principal component analysis (PCA) and canonical correlation analysis (CCA) simplify multidimensional data sets, thus minimizing information loss and enhancing ecological interpretation (Green, 1979). PCA constructs composite variables (components) to maximize explained variance in the 13 original variables. CCA forms pairs of composite variables (canonical variates) to maximize intercorrelation between environmental and invertebrate variables. Both techniques are criticized for assuming linearity among variables (Green and Vascotto, 1978; Poore and Mobley, 1980), but this limitation is not severe when monotonic summary variables are analyzed (Whittaker and Gauch, 1978). Construction of correlation matrices and subsequent PCA and CCA were completed with SPSS (Nie et al., 1975) and BMDP (Dixon et al., 1979) computer packages.

Cluster analysis was used to group stations according to time-averaged invertebrate species composition. The number of species was initially reduced from 102 to 32 by deleting those observed in fewer than 5% of the 272 collections (34 stations by 8 sampling times). Following Boesch (1973), a simultaneous double standardization was performed on the species-by-station data set, and the Canberra Metric was applied to produce a station-by-station dissimilarity matrix. This approach equally weights all 32 species included in the analysis. We grouped stations using the "flexible sorting" strategy of Lance and Williams (1967), with the cluster intensity coefficient set at −0.25. Analysis was conducted with the package of computer programs supplied by Bloom et al. (1977).

Analysis of seasonal trends was limited by irregular sampling intervals (Table 1) caused by equipment breakdowns and inclement weather. Temporal variability in invertebrate abundance and biomass was investigated for each station group identified by cluster analysis. Univariate analysis of variance (ANOVA) was used to test group means over the eight sampling periods.

Results

Macroinvertebrate Distributions

Stations with similar invertebrate composition were grouped by a classification dendrogram (Fig. 2). Species composition in the lower estuary (Group A, Transects III–VI) was distinctly different from that in the upper estuary (Group B, Transects I–II). There appeared to be three subgroupings in the lower estuary. Group A1

Table 1. Eight sampling intervals for 34 stations in the Newport River estuary

Designation		Actual Dates Sampled
1973	Winter	5 Dec 1972–20 Mar 1973
	Summer	26 Jun 1973–18 Jul 1973
	Autumn	3 Oct 1973–15 Nov 1973
1974	Winter	21 Jan 1974–12 Feb 1974
	Spring	17 Apr 1974–16 May 1974
	Summer	22 Jul 1974–12 Aug 1974
	Autumn	15 Oct 1974–18 Nov 1974
1975	Winter	28 Jan 1975– 5 Mar 1975

encompassed Calico Creek (Transect VI) and several stations close to the eastern margin of the lower estuary. Group A2 included stations from the mid-estuary (Transect III) and two stations near the eastern shore of the lower estuary. Group A3 represented the mid-channel and western shore areas (Transects IV–V). These stations were adjacent to natural and dredged channels (Fig. 1) and may be exposed to strong tidal currents.

Characteristic species distributions for the four station groups are given in Table 2. Upper estuary stations (Group B) had abundant populations of small, euryhaline pelecypods, such as *Macoma balthica* and *Mulinia lateralis*, species that thrive in organically-rich muds (Bird, 1970; Parker, 1975). An average of 86% of the invertebrates here were bivalves. The lower estuary was more diverse. Group A1 stations were dominated by polychaetes (48%) and gastropods (28%). Characteristic fauna included *Ilyanassa obsoleta, Tagelus* spp., *Nereis falsa, Amphitrite ornata,* and other species occurring over a wide range of environmental conditions, though most abundant on organic sediments in regions of quiet water. Mid- and lower estuary stations (Groups A2 and A3) were rich in polychaetes (50% and 45%, respectively), crustaceans (26%, 20%), and pelecypods (23%, 34%). Here, dominant species included haustoriids, *Solemya velum, Divaricella quadrisulcata, Dosinia discus, Solen viridis, Nephthys picta, Onuphis microcephala,* and other

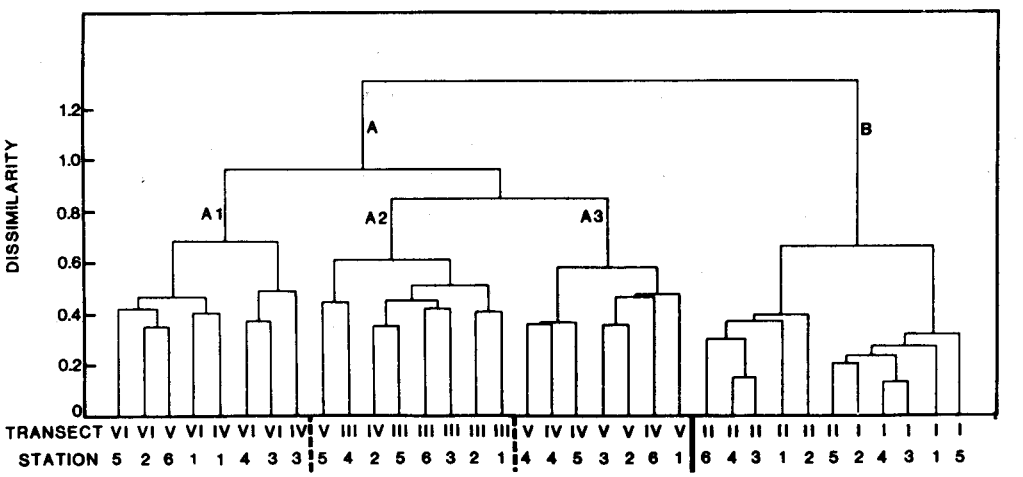


Figure 2. Cluster analysis of 34 stations by invertebrate species composition.

Table 2. Species composition, expressed as average number of each species per n stations, for four groups of stations identified by cluster analysis. Values in parentheses are actual numbers of stations at which a species occurred

Species	Class	Group B (n = 11)	A1 (n = 8)	A2 (n = 8)	A3 (n = 7)
Cerebratulus lacteus	Anopla	0.6 (3)	1.5 (7)	1.3 (7)	0.9 (6)
Ampelisca verrilli	Crustacea	0.6 (4)	7.3 (7)	35.0 (7)	6.0 (7)
Cyathura polita	Crustacea	—	1.0 (5)	1.6 (4)	1.1 (3)
Haustoriidae	Crustacea	0.3 (1)	—	20.5 (7)	5.3 (4)
Upogebia affinis	Crustacea	0.1 (1)	3.3 (7)	1.3 (5)	—
Ilyanassa obsoleta	Gastropoda	0.5 (2)	61.0 (6)	1.8 (2)	0.1 (1)
Nassarius vibex	Gastropoda	0.3 (3)	1.1 (6)	1.0 (5)	—
Macoma balthica	Pelecypoda	15.7 (10)	1.0 (3)	7.1 (5)	0.6 (2)
Macoma tenta	Pelecypoda	8.7 (11)	5.5 (6)	4.5 (8)	2.1 (4)
Mulinia lateralis	Pelecypoda	51.3 (11)	0.8 (3)	5.3 (5)	1.1 (4)
Solemya velum	Pelecypoda	—	0.1 (1)	7.0 (7)	3.7 (4)
Tagelus divisus	Pelecypoda	0.5 (2)	12.6 (6)	5.1 (8)	1.1 (5)
Tagelus plebeius	Pelecypoda	1.4 (1)	15.5 (7)	8.6 (7)	0.1 (1)
Abra aequalis	Pelecypoda	—	1.4 (5)	1.9 (4)	1.1 (3)
Aligena elevata	Pelecypoda	0.3 (1)	—	5.5 (5)	2.9 (4)
Divaricella quadrisulcata	Pelecypoda	—	—	0.5 (2)	4.3 (7)
Dosinia discus	Pelecypoda	—	0.1 (1)	0.8 (3)	2.0 (5)
Mercenaria mercenaria	Pelecypoda	0.2 (2)	1.3 (5)	0.6 (3)	—
Solen viridus	Pelecypoda	—	0.4 (1)	4.4 (8)	1.1 (4)
Tellina versicolor	Pelecypoda	1.2 (6)	1.1 (3)	0.5 (4)	0.7 (3)
Arabella iricolor	Polychaeta	—	6.0 (8)	7.1 (8)	1.3 (5)
Clymenella torquata	Polychaeta	3.3 (7)	16.8 (8)	22.8 (8)	1.3 (6)
Drilonereis magna	Polychaeta	—	4.5 (8)	5.5 (8)	1.3 (5)
Glycera dibranchiata	Polychaeta	2.7 (9)	8.6 (8)	11.6 (8)	7.0 (7)
Haploscoloplos fragilis	Polychaeta	0.4 (4)	2.1 (5)	12.8 (8)	2.9 (6)
Nephthys picta	Polychaeta	0.3 (3)	0.6 (3)	6.3 (7)	3.1 (6)
Nereis falsa	Polychaeta	3.8 (8)	48.6 (7)	12.8 (8)	4.9 (7)
Notomastus hemipodus	Polychaeta	0.6 (1)	12.3 (8)	10.6 (8)	3.9 (7)
Scoloplos rubra	Polychaeta	—	2.3 (3)	8.0 (8)	0.3 (2)
Amphitrite ornata	Polychaeta	—	3.1 (5)	1.0 (4)	0.3 (2)
Onuphis microcephala	Polychaeta	—	0.9 (2)	8.5 (7)	0.6 (3)
Orbinia ornata	Polychaeta	—	0.3 (1)	6.5 (7)	0.9 (4)

species characteristic of sandy environments (Bird, 1970; Gardiner, 1975; Parker, 1975). An analysis of variance of all observations during the study indicated that stations near deep, scoured channels (A3) had significantly ($P < 0.05$) lower invertebrate densities and biomass than the rest of the lower estuary (A1 or A2).

Seasonal trends in numbers and biomass are reported for station groups clustered according to species composition (Fig. 3). Upper estuary stations (Group B) displayed large and significant (ANOVA, $P < 0.05$) differences in abundance and biomass over time. Maximum densities occurred during winter. No statistically significant biomass fluctuations were found in the lower estuary (A1, A2, A3). Although temporal variations in abundance were significant for stations in Groups A2 and A3, density differences were relatively small compared with the upper estuary, and no clear seasonal trends emerged.

Environmental Gradients

Benthic parameters from the Newport River estuary are highly intercorrelated. Of 78 possible Pearson product-moment correlation coefficients, 56 were signif-

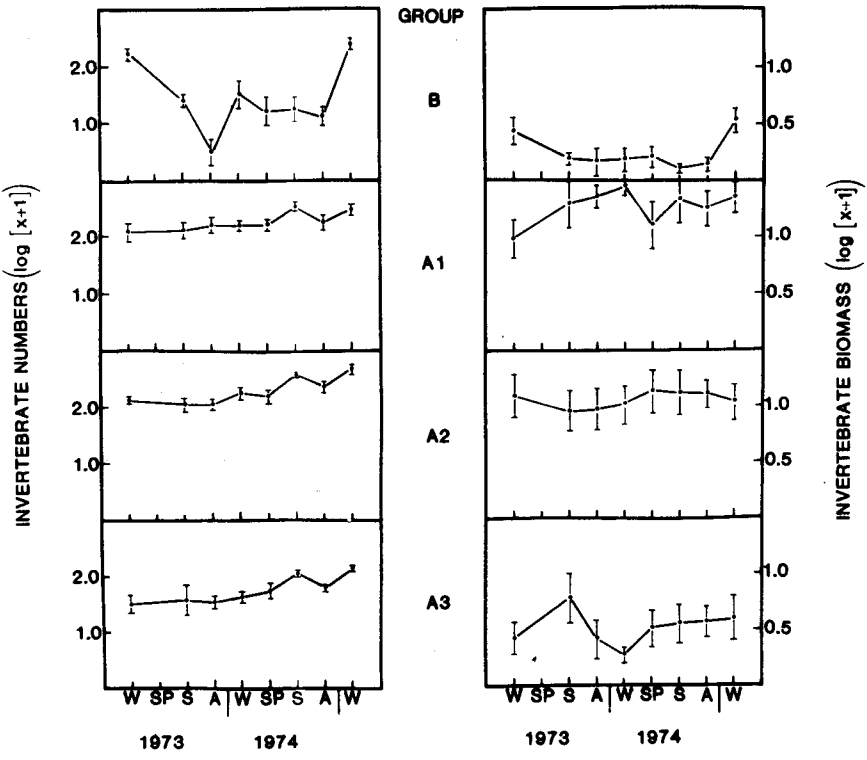


Figure 3. Seasonal distribution of benthic macroinvertebrate density (number m^{-2}) and biomass (g m^{-2}), averaged for groups clustered by species composition. Error bars are ±1 SE.

icant ($P < 0.01$) (Table 3). All parameters were significantly correlated with at least 8 other environmental variables, except for depth (1) and invertebrate numbers (4). The strongest linear relationships ($|r| > 0.70$) occurred within classes of variables (e.g., sediment, microbial, invertebrate) and between the sediment and microbial variables. Although mean salinity was significantly related to 10 other variables, the correlation coefficients were not high. Following this initial analysis, percent silt data were eliminated from further consideration for two reasons. First, inclusion of all three particle size categories is redundant since their sum must equal 100%; second, the virtually perfect negative correlation between sand and silt may make multivariate solutions impossible, since matrices cannot be inverted.

Analysis of the correlation matrix by PCA identified groups of interrelated variables: (1) sediment-microbial, (2) invertebrate and (3) depth. These three components accounted for 87.3% (60.4%, 18.2% and 8.7%, respectively) of the total variance in the 12 original variables (Table 4). Salinity was correlated approximately equally with all three components, reflecting its moderate correlation with most other variables (Table 3). The environmental axis represented by the first component was strongly bipolar. Sand, ATP, and chlorophyll grouped positively at one extreme; clay, organic matter, organic carbon, and pheopigment grouped negatively at the other extreme. This relationship was examined more thoroughly by partitioning the data set. PCA of the seven sediment-microbial

Table 3. Matrix of significant ($P < 0.01$) Pearson correlation coefficients for variables measured in the Newport River estuary, 1972–1975

Variables	D	S	Sand	Silt	Clay	OM	OC	PHEO	ATP	CHL	TN	TB	TS
Depth (D)													
Salinity (S)													
Sediment													
Sand		0.65											
Silt		−0.65	−0.998										
Clay		−0.44	−0.74	0.71									
Organic matter (OM)		−0.69	−0.98	0.97	0.74								
Organic carbon (OC)		−0.68	−0.99	0.98	0.77	0.99							
Pheopigment (PHEO)		−0.59	−0.77	0.76	0.75	0.75	0.81						
Microbial													
ATP		0.43	0.84	−0.84	−0.71	−0.82	−0.84	−0.71					
Chlorophyll *a* (CHL)		0.54	0.82	−0.81	−0.63	−0.84	−0.82	−0.50	0.81				
Invertebrate													
Total numbers (TN)	−0.41									0.49			
Total biomass (TB)		0.64	0.64	−0.65		−0.65	−0.61		0.47	0.67	0.62		
Total species (TS)		0.65	0.65	−0.65	−0.45	−0.65	−0.64		0.53	0.74	0.69	0.80	

Table 4. Principal component analysis of depth, salinity, sediment, microbial, and invertebrate variables measured in the Newport River estuary, 1972–1975

	Composite Variable		
	I	II	III
Depth	0.00	−0.22	0.90
Salinity	0.50	0.59	0.47
Sediment			
Sand	0.89	0.38	0.02
Clay	−0.85	−0.07	−0.14
Organic matter	−0.88	−0.42	−0.03
Organic carbon	−0.91	−0.37	−0.05
Pheopigment	−0.91	0.07	−0.22
Microbial			
ATP	0.87	0.23	−0.27
Chlorophyll *a*	0.70	0.56	−0.20
Invertebrate			
Total numbers	−0.08	0.82	−0.35
Total biomass	0.30	0.87	−0.13
Number of species	0.37	0.87	0.04
Eigenvalue	7.24	2.18	1.05
Percent of total variation explained	60.4	18.2	8.7

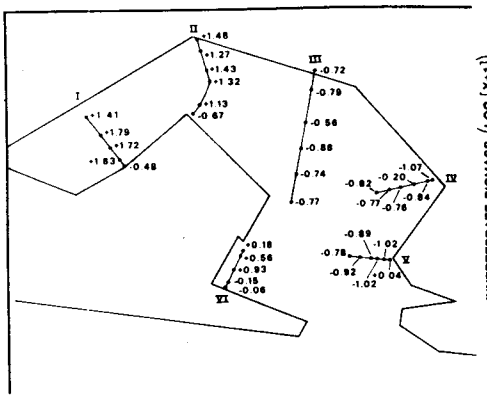
variables resolved a single component accounting for 82.4% of the initial variance (Table 5).

Component scores from PCA of sediment-microbial parameters described bottom types in the Newport River estuary (Fig. 4). Organically-rich, finer sediment bottoms (indicated by large positive scores) occurred in the upper estuary; sandy sediments, rich in ATP and chlorophyll, (high negative scores) occurred in the lower estuary and extreme southern shore of the upper estuary. Estuarine sediments of Calico Creek and areas along the eastern shore of the lower estuary had intermediate sediment-microbial properties.

Invertebrate variables were plotted against sediment-microbial component scores for each station. Reduced biomass (Fig. 5) and low numbers of species and in-

Table 5. Principal component analysis of sediment and microbial variables measured in the Newport River estuary, 1972–1975

Variable	Composite Variable I
Sediment	
Sand	−0.97
Clay	0.84
Organic matter	0.97
Organic carbon	0.98
Pheopigment	0.83
Microbial	
ATP	−0.90
Chlorophyll *a*	−0.85
Eigenvalue	5.77
Percent of total variation explained	82.4



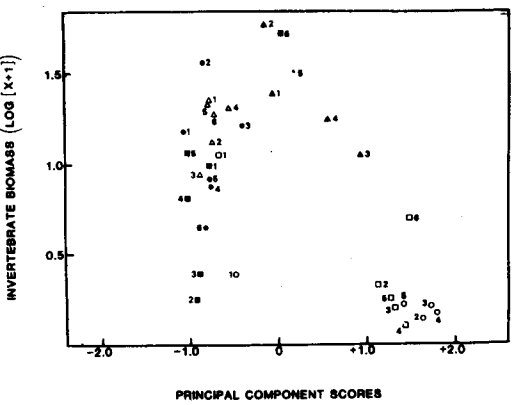


Figure 4. (Left) Schematic diagram of the Newport River estuary with principal component scores based on the sediment-microbial characteristics of 34 sampled stations.

Figure 5. (Right) Total macroinvertebrate biomass (g m^{-2}) plotted against principal component scores from sediment-microbial analysis of 34 stations. Transects are denoted: I, ○; II, □; III, △; IV, ●; V, ■; VI, ▲. Numerals indicate stations within transects.

dividuals were associated with anaerobic, organically-rich, fine sediments of the upper estuary. Sandy bottom areas with high ATP and chlorophyll concentrations generally had higher macrofaunal biomass. Exceptions to this trend were Station I-1 (southern station at the uppermost transect), which may be exposed to high currents and low salinities, and Stations IV-4, 5, 6, and V-2, 3, 4 (Group A3 of cluster analysis) which had very low pheopigment content and may be affected by high tidal velocities in adjacent deep channels (Fig. 1).

Table 6. Canonical correlation between original sediment, microbial, and invertebrate variables and the first two canonical variates. The canonical correlation coefficient, significance level, redundancy statistic, and proportion of variation in each invertebrate variable (R^2; multiple regression) associated with all sediment-microbial variables are given

Source Variables	CV I	CV II	R^2
Set I			
Mean salinity	0.78	−0.32	
Sand	0.79	−0.36	
Clay	−0.42	0.57	
Organic matter	−0.79	0.26	
Organic carbon	−0.76	0.35	
ATP	0.58	−0.16	
Chlorophyll *a*	0.78	0.06	
Pheopigment	−0.34	0.71	
Set II			
Invertebrate biomass	0.95	0.27	0.83*
Number of individuals	0.54	0.71	0.55*
Number of species	0.92	0.02	0.79*
Canonical correlation	0.93	0.68	
Significance	<0.000	0.006	
Redundancy	0.59	0.09	0.72†

* Significant ($P < 0.01$).
† Total redundancy for invertebrate data given sediment-microbial variables.

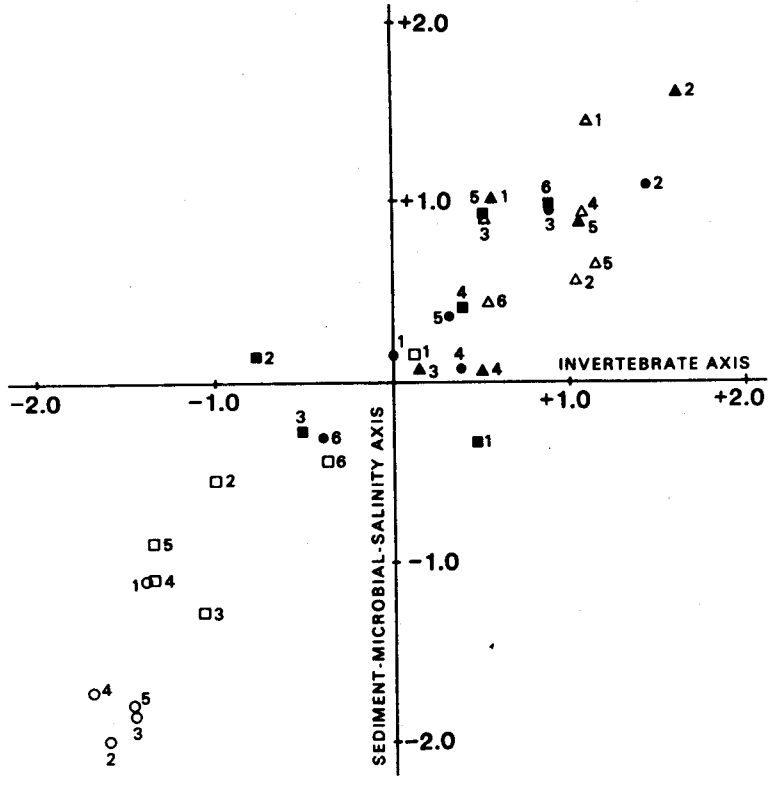


Figure 6. Canonical variate scores between invertebrate variables and sediment-microbial-salinity variables. The canonical correlation coefficient is 0.93. Transects are denoted: I, O; II, □; III, △; IV, ●; V, ■; VI, ▲. Numerals indicate stations within transects.

Analysis of the relationship between invertebrate variables and environmental factors by CCA identified two canonical variates (CVs) having significant canonical correlation coefficients of 0.93 and 0.68, respectively (Table 6). A total redundancy (Stewart and Love, 1968) of 0.72 meant that 72% of the variation in invertebrate variables was associated with variations in salinity, sand, clay, organic matter, organic carbon, pheopigment, ATP, and chlorophyll. Of this total redundancy, 94% (i.e., 0.56 for CV I and 0.09 for CV II) was accounted for by the two pairs of canonical variates.

The first canonical relationship (CV I) was interpreted as ordering invertebrate variables, especially biomass and numbers of species, along an environmental continuum represented by sediment-microbial bottom type and associated upstream salinity gradient (see Fig. 6 for plot of CV I scores). High invertebrate values occurred in areas of high salinity, sand, ATP, and chlorophyll, and low clay, organic matter, organic carbon, and pheopigment. These conditions existed in the lower estuary. Opposite conditions in the upper estuary were associated with low invertebrate scores. In contrast to CV I, the second canonical relationship (CV II) related high numbers of invertebrates to areas of relatively high clay and pheopigment. These conditions existed in Calico Creek and near marshes along the eastern border of the estuary.

Table 7. Sediment-microbial data by station for each of four groups of stations identified by cluster analysis. Salinity is in ppt.; sand, clay, organic matter (OM), and organic carbon (OC) are percent of dry weight; ATP and chlorophyll *a* (CHL) are in mg/m³; pheopigment (PHEO) is in mg/m². Within each group, stations are ordered according to the rank of their principal component scores from analysis of sediment-microbial variables

Group	Trans.	Sta.	Salinity	Sand	Clay	OM	OC	ATP	CHL	PHEO	Component Score Rank
B	II	1	27.5	93.2	5.2	0.86	0.35	1.98	2.65	8.9	16
	I	1	22.5	88.1	7.0	1.03	0.51	2.45	2.33	9.4	18
	II	2	28.0	46.6	8.4	4.55	2.51	0.50	1.18	17.8	26
	II	5	27.0	36.8	9.0	6.46	3.79	0.80	1.23	16.2	27
	II	3	27.9	29.3	8.7	5.74	3.00	0.49	1.15	16.3	28
	I	5	23.4	28.9	8.6	8.10	4.27	0.69	1.28	15.7	29
	II	4	27.1	28.2	8.6	7.61	3.52	0.55	1.15	16.8	30
	II	6	26.3	53.9	13.5	6.16	3.25	0.54	0.92	15.9	31
	I	2	23.0	15.6	9.1	10.39	4.73	1.11	0.83	16.8	32
	I	3	23.8	20.7	11.8	9.17	4.60	1.06	0.73	17.0	33
	I	4	24.9	19.6	12.2	8.95	4.67	0.79	0.84	17.3	34
A1	IV	1	30.8	89.1	5.1	0.80	0.36	2.57	5.33	5.8	1
	IV	3	31.8	86.5	7.2	1.68	0.63	1.32	2.71	9.7	19
	VI	2	32.1	88.8	7.6	1.43	0.56	1.69	2.18	13.5	20
	VI	1	31.7	82.6	9.6	1.70	0.82	1.72	2.95	11.5	21
	V	6	33.1	84.8	9.1	1.60	0.60	1.03	2.15	9.7	22
	VI	5	30.7	76.9	12.6	2.13	1.04	1.68	3.38	12.8	23
	VI	4	31.6	59.7	10.5	2.44	1.62	1.18	1.84	12.8	24
	VI	3	32.0	43.7	7.8	4.49	2.90	0.77	1.68	15.3	25
A2	V	5	33.4	93.7	4.5	0.82	0.25	2.43	3.38	5.7	3
	III	3	29.1	92.6	5.0	1.23	0.42	2.38	5.04	9.1	6
	IV	2	31.1	88.8	5.8	1.05	0.43	2.92	4.59	9.8	7
	III	5	28.9	93.8	4.5	0.84	0.41	1.91	3.63	9.3	9
	III	1	31.6	91.1	6.2	1.23	0.45	2.91	4.09	9.9	11
	III	2	30.3	92.4	5.1	1.13	0.41	1.75	3.70	7.2	14
	III	6	27.2	91.6	6.0	0.90	0.45	2.16	4.31	10.0	15
	III	4	29.4	92.7	5.2	1.17	0.34	1.68	3.06	10.7	17
A3	V	4	31.9	93.4	4.2	0.82	0.28	2.58	2.86	5.2	2
	V	2	31.6	92.3	5.5	0.91	0.29	2.42	2.87	4.7	4
	V	3	31.8	93.6	4.7	1.45	0.30	2.11	1.95	2.9	5
	IV	6	32.2	91.9	5.0	0.85	0.24	1.93	1.85	3.7	8
	V	1	31.9	92.0	5.5	1.22	0.33	2.02	1.89	3.3	10
	IV	5	32.1	89.1	6.5	1.00	0.33	1.80	4.29	5.8	12
	IV	4	32.1	91.7	4.9	0.90	0.30	1.79	2.24	4.9	13

Discussion

Differences in invertebrate abundance, biomass, and species composition were accompanied by changes in the physico-chemical character of sediments in the Newport River estuary. Upper and lower estuary stations had distinct invertebrate communities (Groups B and A of cluster analysis) and sediment-microbial properties (PCA component scores) (Table 7). Generally, the upper estuary had fine, organically-rich sediments (highest PCA scores); the lower estuary had coarser, less organic sediments (lowest PCA scores). Two stations along the southern shore (I-1, II-1) were exceptions. Each had sediment-microbial properties similar to the lower estuary, but resembled the upper estuary in species composition, probably because frequent exposure to low salinities limited colonization to extremely euryhaline forms. Dominant upper estuary species, such as *Mulinia lateralis,* are thought to have low competitive fitness, but thrive where adverse conditions,

such as highly reducing sediments or extreme salinity fluctuations, exclude other organisms (Parker, 1975). Species inhabiting the lower estuary generally are not as tolerant of rapid salinity changes and prefer sandy, aerobic sediments. Reduced salinity and extremely organic (>3% carbon), fine sediments of the upper estuary were associated by CCA (CV I) with relatively low biomass and numbers of species (Table 6, Fig. 6). Greater biomass and species richness were associated with higher salinity and lower organic matter in sandy sediments of the lower estuary.

Within the lower estuary, stations were subdivided into three groups (A1, A2, A3 of cluster analysis) according to species composition. One group, Calico Creek and eastern border stations (A1), had sediment-microbial properties (PCA scores) intermediate to the upper estuary and remaining lower estuary stations (Table 7, Fig. 4). These areas were characterized by species favoring organic sediments, especially in relatively saline, quiescent waters. The only exception, Station IV-1, was near a domestic seawall and may be unrepresentative. The remaining lower estuary stations (Groups A2, A3) had lowest sediment-microbial scores and were characterized by species preferring sandy environments. These two station groups could not be separated by sediment-microbial scores. All three station groups, however, could be differentiated by considering CCA results (Table 6) and reexamining the time-averaged data (Table 7). The second canonical variate (CV II) related invertebrate densities to the quantity of decomposing plant matter (pheopigment) in the sediments. Stations in shallow, depositional areas adjacent to salt marshes (A1) had relatively fine, organic (>0.5% carbon) sediments and large invertebrate populations; stations adjacent to deep channels scoured by tidal currents (A3) had relatively sandy, organically-poor (≤0.3% carbon) sediment and few invertebrates. The remaining stations (A2) were intermediate and could be distinguished from Group A3 by their higher invertebrate densities (Table 2, Fig. 3) and concentrations of pheopigment, organic carbon, and chlorophyll (Table 7).

Seasonal patterns of abundance and biomass varied in the estuary, possibly because of differential predation on the dominant species. In the lower estuary, where no pronounced seasonal trends were observed, communities were dominated by deep-living polychaetes and bivalves that may be less susceptible to epibenthic predators (Holland et al., 1980). In the upper estuary, marked seasonal trends were largely determined by the population dynamics of *Mulinia lateralis*. Densities of this rapidly growing bivalve (Calabrese, 1970) were high in winter and early spring, and low in summer. *M. lateralis* is exceptionally tolerant to a wide range of environmental conditions (Parker, 1975), but is highly vulnerable to predation by blue crabs and spot (Virnstein, 1977; 1979), two of the most important predators in the Newport River estuary (Kjelson et al., 1978). Blue crabs become inactive, and other nektonic predators migrate to deeper water during early winter (Hyle, 1976). Decreased predation pressure is a likely explanation for winter increases observed in the upper estuary.

The observed sediment distributions were consistent with results of earlier studies (Johnson, 1959; Brett, 1963; Bird, 1970). Fine to medium sands were found in the lower estuary and southern shore of the upper estuary. Silty muds dominated most of the upper estuary and, to a lesser extent, Calico Creek. Bird (1970) described two major mollusc communities within the estuary and differentiated them into upper and lower estuary forms on the basis of salinity and sediment type. Ferguson and Murdoch (1975) also recognized two distinct environmental regions and used the concepts of estuarine sand microbiocenosis and sulphuretum (Fenchel, 1969) to describe sediment-microbial communities in the estuary. Estuarine sand microbiocenosis was defined as an oxidized layer of sand

and detritus, 1–10 cm thick, overlying the reduced zone of the sulfide system. The sulphuretum was characterized by highly reducing surface sediments, rich in silt and organic matter. We found these two habitats to be opposite extremes of an environmental continuum encompassing a range of sediment-microbial properties. Distinct macrofaunal communities of the upper estuary, Calico Creek, and the lower estuary could be positioned along this estuarine gradient. Within the lower estuary, however, intergroup differences were more subtle. At these locations, a second environmental gradient, expressing the degree of local organic input and tidal current velocity (i.e., shallow, depositional areas near salt marshes vs. deep, tidally scoured channels), appeared to be an important factor regulating invertebrate species distribution.

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Literature Cited

Biernbaum, C. K. 1979. Influence of sedimentary factors on the distribution of benthic amphipods of Fishers Island Sound, Connecticut. J. Exp. Mar. Biol. Ecol. 38: 201–223.

Bird, S. O. 1970. Shallow-marine and estuarine benthic molluscan communities from area of Beaufort, North Carolina. Am. Assoc. Pet. Geol. Bull. 54: 1651–1676.

Birkett, L. and A. D. McIntyre. 1971. Treatment and sorting of samples. Pages 156–168 *in* N. A. Holme and A. D. McIntyre, eds. Methods for the study of marine benthos. I.B.P. Handbook No. 16. Blackwell Scientific Publications, Oxford.

Bloom, S. A., S. L. Santos and J. G. Field. 1977. A package of computer programs for benthic community analyses. Bull. Mar. Sci. 27: 577–580.

Boesch, D. F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. Mar. Biol. 21: 226–244.

Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. 42: 225–229.

Brett, C. E. 1963. Relationships between marine invertebrate infauna distribution and sediment type distribution in Bogue Sound, North Carolina. Ph.D. Thesis, University of North Carolina, Chapel Hill. 202 pp.

Calabrese, A. 1970. Reproductive cycle of the coot clam, *Mulinia lateralis* (Say), in Long Island Sound. Veliger 12: 265–269.

Clifford, H. T. and W. Stephenson. 1975. An introduction to numerical classification. Academic Press, New York. 229 pp.

Dixon, W. J., M. B. Brown, L. Engelman, J. W. Frame and R. I. Jennrich. 1979. Biomedical computer programs p-series. University of California Press, Berkeley. 880 pp.

Fenchel, T. M. 1969. The ecology of marine microbenthos. IV. Structure and function of the benthic ecosystem, its chemical and physical factors and the microfauna communities with special reference to the ciliated protozoa. Ophelia 6: 1–182.

Ferguson, R. L. and M. B. Murdoch. 1975. Microbial ATP and organic carbon in sediments of the Newport River estuary, North Carolina. Pages 229–250 *in* L. E. Cronin, ed. Estuarine research, vol. 1. Academic Press, New York.

Gardiner, S. L. 1975. Errant polychaete annelids from North Carolina. J. Elisha Mitchell Sci. Soc. 91: 77–220.

Goodall, D. W. 1978. Numerical classification. Pages 247–286 *in* R. H. Whittaker, ed. Classification of plant communities. Dr. W. Junk, The Hague.

Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. Wiley, New York. 257 pp.

——— and G. L. Vascotto. 1978. A method for the analysis of environmental factors controlling patterns of species composition in aquatic communities. Water Res. 12: 583–590.

Holland, A. F., N. K. Mountford, M. H. Hiegel, K. R. Kaumeyer and J. A. Mihursky. 1980. Influence of predation on infaunal abundance in upper Chesapeake Bay, USA. Mar. Biol. 57: 221–235.

Hughes, R. N. and M. L. H. Thomas. 1971. Classification and ordination of benthic samples from Bedeque Bay, an estuary in Prince Edward Island, Canada. Mar. Biol. 10: 227–235.

Hyle, R. A. 1976. Fishes of the Newport River estuary, North Carolina, their composition, seasonality, and community structure, 1970–1972. Ph.D. Thesis, University of North Carolina, Chapel Hill. 192 pp.

Ivester, M. S. 1980. The distribution of meiobenthic copepods along a sediment gradient: factor and niche analyses. Bull. Mar. Sci. 30: 634–645.

Johnson, F. K. 1959. The sediments of the Newport River estuary, Morehead City, North Carolina. M.S. Thesis, University of North Carolina, Chapel Hill. 36 pp.

Kjelson, M. A. and G. N. Johnson. 1978. Catch efficiencies of a 6.1-meter otter trawl for estuarine fish populations. Trans. Am. Fish. Soc. 107: 246–254.

———, ———, G. W. Thayer and R. L. Ferguson. 1978. Preliminary summary of estimations of nekton biomass in the Newport River estuary. Pages 237–266 *in* Annual report to the U.S. Department of Energy. U.S. National Marine Fisheries Service, Southeast Fisheries Center, Beaufort, N.C.

Lance, G. N. and W. T. Williams. 1967. A general theory of classificatory sorting strategies. I. Hierarchical systems. Comput. J. 9: 373–380.

Mills, E. L. 1975. Benthic organisms and the structure of marine ecosystems. J. Fish. Res. Board Can. 32: 1657–1663.

Moore, C. G. 1979. The identification of faunal gradients and associations of meiobenthic copepods by multivariate analyses. J. Mar. Biol. Assoc. U.K. 59: 725–736.

Morgans, J. F. C. 1956. Notes on the analysis of shallow water soft substrata. J. Anim. Ecol. 25: 367–387.

Mountford, N. K., A. F. Holland and J. A. Mihursky. 1977. Identification and description of macrobenthic communities in the Calvert Cliffs region of the Chesapeake Bay. Chesapeake Sci. 18: 360–369.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner and D. H. Bent. 1975. Statistical package for the social sciences. McGraw-Hill, New York. 675 pp.

Parker, R. H. 1975. The study of benthic communities. Elsevier, Amsterdam. 279 pp.

Poore, G. C. and M. C. Mobley. 1980 Canonical correlation analysis of marine macrobenthos survey data. J. Exp. Mar. Biol. Ecol. 45: 37–50.

Rice, T. R. and R. L. Ferguson. 1975. Response of estuarine phytoplankton to environmental conditions. Pages 1–43 *in* F. J. Vernberg, ed. Physiological ecology of estuarine organisms. University of South Carolina Press, Columbia.

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco. 776 pp.

Stewart, D. and W. Love. 1968. A general canonical correlation index. Psychol. Bull. 70: 160–163.

Thayer, G. W., W. E. Schaaf, J. W. Angelovic and M. W. LaCroix. 1973. Caloric measurements of some estuarine organisms. U.S. Natl. Mar. Fish. Serv. Fish. Bull. 71: 289–296.

———, R. B. Williams, T. J. Price and D. R. Colby. 1975. A large corer for quantitatively sampling benthos in shallow water. Limnol. Oceanogr. 20: 474–481.

Virnstein, R. W. 1977. The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. Ecology 58: 1199–1217.

———. 1979. Predation on estuarine infauna: response patterns of component species. Estuaries 2: 69–86.

Whittaker, R. H. and H. G. Gauch. 1978. Evaluation of ordination techniques. Pages 277–336 *in* R. H. Whittaker, ed. Ordination of plant communities. Dr. W. Junk, The Hague.

Williams, R. B., M. B. Murdoch and L. K. Thomas. 1968. Standing crop and importance of zooplankton in a system of shallow estuaries. Chesapeake Sci. 9: 42–51.

Wolfe, D. A. 1975. Modeling the distribution and cycling of metallic elements in estuarine ecosystems. Pages 645–671 *in* L. E. Cronin, ed. Estuarine research, vol. 1. Academic Press, New York.

———, F. A. Cross and C. D. Jennings. 1973. The flux of Mn, Fe, and Zn in an estuarine ecosystem. Pages 159–175 *in* Radioactive contamination of the marine environment. International Atomic Energy Agency, Vienna.

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ADDRESS: *National Marine Fisheries Service, NOAA, Southeast Fisheries Center, Beaufort Laboratory, Beaufort, North Carolina 28516-9722.*